Carbon and Energy Flow in Terrestrial Ecosystems: Relevance to Microflora

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Over the past 20 years, "production" ecology has concentrated on quantifying plant and animal production in different ecosystems. Much of the research has been field orientated and has been at a scale of resolution to which microbial ecology has had difficulty in relating, namely, the scale of space (kilo rather than micro) and time (centuries and years rather than days or hours). More recently, production ecology has turned toward nutrient and population dynamics and toward the growth strategies of organisms, areas in which the microbial ecologist can both contribute and gain. None of the fields is actually new; rather, they show recurrent phases in which new information in one field stimulates interest in another.

Here we wish to summarize some of the information arising from ecosystem and productivity studies with possible relevance to microbial ecology. In particular, the pattern of primary production in different systems is now reasonably established, and we explore the extent to which plant production influences the microflora, and also the fauna, populations in the heterotrophic system. An initial premise is that the composition and activity of the microflora are determined by three groups of factors: climate, soil conditions, and resource quality (80). It is mainly through variation in resource quality that microbial populations may be expected to reflect vegetation patterns, but the microflora may also be expected to show responses in common with the plants to external environmental conditions.

NET PRIMARY PRODUCTION

Quantity. If we ignore the small proportion of carbon and energy fixation by autotrophic microflora, the main pattern of primary production in different ecosystems is largely as outlined by Whittaker (88), developed from the compilation of Bray and Gorham (10), Rodin and Bazilevitch (68), and others. This has been amplified in more recent syntheses of International Biological Program (IBP) and related ecosystem data (7, 11, 18, 30, 31, 67). The general relationship with climate is clear, reflecting both its intensity and variability (Table 1). There are still some reservations or anomalies in these results, including some exceptionally high production rates: 50 to 60 t/ha per year in sub-Antarctic systems (89) and >10 t/ha per year in some deserts (87). Also, there is an increasing body of evidence that fine root production and root exudation are underestimated components of earlier production estimates (21, 54, 64). For example, it has been estimated that fine root production in certain forest stands is about equivalent to leaf litter input (54). Production in tropical systems is still poorly quantified, with belowground estimates being largely neglected.

The production values given are for ecosystems which approximate to steady state and therefore represent equivalent input to the heterotrophic or decomposition subsystem. In successional stages, up to steady state, net production will be greater than litter input to decomposition (the system is aggrading), whereas postmaturity litter fall will be greater than net production as a result of loss of accumulated biomass, i.e., a degrading system. (The term litter is used to include all inputs from plant production unless qualified.)

Quality. Most of the production data are expressed as dry weights by species or parts of species (leaves, roots, etc.), with little reference to their chemical composition; yet, it is composition, in terms of structural and storage carbohydrates, nutrient content, and secondary compounds, which is important to the microflora.

A first approximation to estimation of variation in quality of input to decomposition (Table 1) is given by fractionating into leaves (nonwoody), roots, and wood on the basis that this is, first, the lowest common denominator between data sets and, second, that it represents high, medium, and low quality, respectively, through increasing lignin and decreasing nutrient concentrations. Interpretation is necessarily limited by the very simplified nature of the information, but several features emerge. The dominance of wood in forests has less effect on decomposer input than might be expected, because although wood may constitute 70 to 80% of the biomass, its proportion of the litter input is much smaller. For example, wood constituted 50% of litter in an old stand of *Pseudotsuga menziesii* and only about 2% in a young stand (19). Wood is also a significant proportion of input in many dwarf shrub tundra, chaparral, and savannah systems. Additionally, the major

TABLE 1. Net primary production (NPP, tonnes per hectare per year) according to biomes and proportionate allocation to above- and belowground biomass (from 18, 20, 62, 80, 84, 87, 89)

	Mean NPP	Minimum–maximum (*n*)	Proportions of above- and belowground biomass		
			Above		Below, root
			Nonwoody	Woody	
Tundra (sub-Antarctic)	4.0	0.7–8.9 (18)	30	—	60
	58.0	55.8–60.2 (2)			
Temperate forest	13.0	4.4–19.0 (15)	60	20	20
Temperate grassland	15.0	7.0–34.7 (38)	40	—	60
Desert	2.0	0.5–7.8 (21)	30	10	60
Tropical forest	17.0	9.4–28.0 (3)	60	20	20

input of roots, both large and small, in nonforest systems reflects the different growth characteristics of the plants, with roots representing a storage, transport, and support system characterized by a high proportion of structural polysaccharides and low nutrient concentration, more similar to woody tissues than to many leaves.

However, the composition of different fractions is not as clearly distinct as it initially appears. In general, wood is slightly higher in lignin and cellulose, being lower in soluble carbohydrate, nitrogen, and phosphorus than are roots and leaves. The range is very wide for all litter types, and certain of the analytical techniques are of dubious comparability.

The reasons for the more restricted variation in composition than in quantity are (i) withdrawal of soluble organic fractions before death, (ii) withdrawal of soluble nutrients, mainly N, P, and K before death, and (iii) varying dry matter production per unit of nutrient uptake. The composition of root material at death, and of root exudates, is poorly known. For example, the nutrient contents of root material quoted in the literature usually refer to live roots, but a considerable degree of resorption is likely to occur before death. Estimates of the approximate input of structural and soluble carbohydrates (Table 2) suggest that, although amounts differ considerably between biomes, the proportions vary little. The dominance of high-molecular-weight fractions is overwhelming.

Some important differences are not reflected in Table 2. Secondary compounds, such as phenols and terpenes, are developed in perennial tissues of plants in late succession and in severe environments as "defense" against herbivory or attack by parasites. Such compounds are known to influence populations of decomposer microflora and fauna, often as inhibitors (43, 70) but also as substrates (61). Spatial configuration of the litter resource, including factors such as surface area-to-volume ratios, and spatial separation of nutrient sources in a resource are also variants in quality.

The implication of the foregoing is that any ecosystem will contain a wide range of substrates available to the decomposers and that dominance of a particular quality of substrate in an ecosystem is more apparent than real (Table 2). During succession the proportion of structural carbohydrates will be lower as biomass accumulates. It must also be appreciated that under certain conditions the quality and quantity of an input may increase considerably, e.g., at felling, at climatic death due to drought, or with herbivore population fluctuations, providing a resource rich in nutrients and soluble carbohydrates because of a lack of premortality resorption. Conversely, after fire carbon may be both severely limited and markedly changed.

TABLE 2. Preliminary estimates of substrate input to the decomposer subsystem in different biomes (tonnes per hectare per year)[a]

Biome	Lignin (SD)	Cellulose (SD)	Soluble carbohydrate (SD)
Tundra	1.4 (1)	2.3 (1.6)	0.2 (0.1)
Temperate forest	3.7 (1)	4.7 (1.3)	0.8 (0.2)
Temperate grassland	4.7 (1)	8.2 (1.7)	0.7 (0.1)
Desert	0.6 (1)	1.1 (1.8)	0.1 (0.0)
Tropical forest	4.8 (1)	6.3 (1.3)	0.7 (0.1)

[a] Amounts are calculated on the basis of primary production data in Table 1 and litter substrate concentrations in the literature (19, 39, 45, 80, 83, 86). Mean concentration values from different litter types were used, but it must be emphasized that these are very variable and the calculation is tentative.

DECOMPOSITION

Variation between biomes. Only a small fraction of the net primary production is consumed and respired by herbivores, and at least 90% is transferred to the decomposer system directly or via feces and death. Although much effort has concentrated on measurement of aboveground

litter fall, the best estimates of input to decomposition are of net primary production, especially in the relatively stable systems that have been intensively studied, because they reflect belowground production. Turnover of the organic horizons may be relatively rapid (Table 3), but the majority of dead organic matter is within the mineral soil (70 to 80% in tundra, boreal, and temperate forest; more than 90% in temperate grasslands, deserts, and tropical forests). Turnover of the total dead organic matter pool may take many decades, although the decay of resistant fractions takes centuries (25). As with primary production there is a general increase in decomposition rate with temperature. The limitation of moisture in deserts is not as clear as might be expected in the surface litter, possibly because of physical losses or rapid decomposition during moist periods. However, in the more detailed analyses the shift in control of decomposition from temperature to moisture within grassland moisture gradients is clear (16). Even in apparently cold-dominated biomes, low moisture levels can retard microbial activity (13, 38), and the interaction of temperature and moisture is expressed in the general relationship of decomposition to evapotranspiration (55).

Influence of substrate quality. The broad biome pattern masks the wide range of variation in rates of decomposition, and there is considerable overlap between biomes, including tropical and temperate forests (J. M. Anderson and M. J. Swift, *in* S. L. Sutton, T. C. Whitmore, and A. C. Chadwick, ed., *The Tropical Rain Forest*, in press). In addition, major variation in activity results from variation in substrate quality within a biome. The initial rates of decay, measured by weight loss or respiration of litters, frequently show the fastest rates to be 5 to 10 times that of the slowest, even among leaf litters within a site (e.g., 39, 58, 83). The slow decay rate of woody fractions emphasizes the point, but there is also increasing evidence that decay rates of roots also tend to be slower than that of the associated leaves (17,.54; B. Berg, Ecology, in press). Decomposition of naturally dying roots is probably lower than that reported in many decomposition studies which use live roots, initial losses of fresh material being higher than that of naturally dead litter through lack of resorption of soluble fractions (6).

The term substrate quality lacks definition. It is the combination of physical and chemical attributes of a resource which determines its potential for microbial growth. No single factor determines quality. Even though nitrogen and lignin concentration provide a general correlation with resource decomposition (4, 24, 39), this reflects the intercorrelation of a number of components, particularly between structural and nonstructural carbohydrates, which provide the main carbon and energy source, and essential nutrients (70). An additional effect on microbial activity comes from secondary compounds developed by the plants as defense against herbivores or pathogens. The influence of the comprehensive research into plant defense compounds (69) has not been fully felt in decomposition research, although there is increasing definition of chemical changes during decomposition (3, 6, 36, 71, 73, 74).

One key feature is that the chemical factors which control decomposition change with time; Berg and Staaf (4) showed the shift from nutrient to carbon substrate control in Scots pine needles and the interaction between nitrogen and lignin. Differences in control between resources are to be expected, as noted by McClaugherty, Aber, and Melillo (54) in relation to decomposition of fine roots and leaves. Surface area to volume, the surface characteristics, and the spatial arrangement of the substrates and nutrients are additional physical factors which modify decomposition rate through their influence on microbial colonization, establishment, and growth (78).

Thus, the pattern of heterotrophic carbon and energy flow across biomes is dominated by a broad climatic trend within which there is a finer

TABLE 3. Primary production, organic matter standing crops, and turnover in major biomes[a]

Biome	Net primary production (t ha^{-1} yr^{-1})	Litter input (t ha^{-1} yr^{-1})	Standing dead (t ha^{-1})	Litter (t ha^{-1})	Soil organic matter[b] (t ha^{-1})	K_L[c]	K_T[c]
Tundra	4.0	1.7	1.8	28.0	200.0	0.06	0.017
Boreal forest	8.0	5.8	1.3	35.0	150.0	0.17	0.043
Temperate forest	13.0	8.5	7.9	30.0	120.0	0.28	0.082
Temperate grassland	15.0	7.3	—	4.0	220.0	1.78	0.065
Desert	2.0	1.3	—	1.0	80.0	1.30	0.025
Tropical forest	17.0	15.8	13.5	7.5	85.0	2.11	0.160

[a] From references 1, 18, 20, 32, 72, 80, 84, 87, 89, and Anderson and Swift (in press).

[b] Schlesinger (72) gives approximately double the amounts quoted by Ajtay, Ketner, and Duvigneaud (1) for all biomes except desert.

[c] K_L = litter input ÷ litter; K_T = net primary production ÷ standing dead + litter + soil organic matter.

pattern related to substrate quality.

Microflora and fauna populations. The influence of these determinants of the heterotrophic populations is less clearly seen because comparative information on microflora and fauna between ecosystems is particularly sparse and bedevilled by problems of comparable methods. However, a number of general points do emerge, making particular use of the compilation and analysis of IBP data given by Petersen and Luxton (65) and Kjøller and Struwe (49). The majority of comparable data for microbial communities is mycological and shows that species composition is clearly related to biome type, even for the same biome in different continents (22, 49; M. Christensen, Int. Mycol. Congr., 2nd, 1977, Abstr. vol. A–L, p. 99). Comparative biomass estimates are few, yet there is some indication of up to 180 g of total fungal biomass per m^2 in temperate grasslands, compared with upper levels of 120 g/m^2 in temperate forests and up to 20 g/m^2 in tundra (49).

Estimates of microbial production are largely based on estimates of the input of organic matter, microbial yield coefficient, maintenance, and biomass. Earlier suggestions that the carbon/energy input was insufficient to allow more than a generation or so of the microflora per annum (33, 44) have been replaced by an estimated turnover (production/biomass) of 5 to 18 generations for tundra (23, 49) and up to 50 for temperate forests (40, 49, 59). Although speculative, these estimates recognize the recycling of microbial biomass and the high yield efficiency of the microflora, even when growing on natural substrates. Thus, if one discounts winter and periods of drought, the "generation times" are of the order of days.

Bacterial populations show changes both in species composition and in functional activity between ecosystems. Sundman (76) demonstrated, for example, that the characters of bacterial soil populations change markedly with plant cover type. She compared forest humus, grassland, and field soils, concluding that a "*Bacillus*" factor characterized isolates from forest humus.

The major faunal groups and faunal biomass show a fairly distinct pattern of biomass and composition between ecosystems (65, 80): tundra, 3.3 g/m^2, enchytraeids and dipterous larvae; temperate coniferous forest, 2.4 g/m^2, microarthropods and enchytraeids; temperate deciduous forest, 8.0 g/m^2, large oligochaetes; temperate grassland, 5.8 g/m^2, large oligochaetes; and tropical grassland and forest, 1.9 g/m^2, isoptera. O'Neill and DeAngelis (62) suggested that the faunal (heterotrophic) biomass expressed as a proportion of primary production is inversely related to accumulated organic matter. This indicates that, despite the low contribution of fauna directly to decomposition, they either stimulate microbial decomposition (2) or are correlated with it. The result is rapid organic matter turnover and nutrient recycling where the faunal contribution is maximal.

It is only in temperate deciduous forests and grasslands that macrofauna are dominant, and it is therefore only in these systems that physical disturbance of the soil and comminution of litter is a major process. In tundra the relatively large biomass masks a low production because of the long generation times of the dipterous larvae. The dominance of enchytraeids, particularly the parthenogenetic *Cognettia sphagnetorum*, in these environments may reflect an adaptation to stress conditions. Despite the low faunal biomass of tropical forests and grasslands, the dominant termites show high productivity and have developed a highly competitive system with maximum spatial dominance, environmental control within termitaria, and intimate symbiotic relationships with fungi (50). There is no particular direct evidence relating faunal biomass or production to quality of organic matter input; rather, they appear to reflect responses to the environment.

MICROBIAL GROWTH STRATEGIES WITHIN AND BETWEEN ECOSYSTEMS

The preceding review, while identifying the broad pattern of carbon and energy flow, has lacked direct relevance to the scales of time and space of microbiology and does little to distinguish patterns applicable to the taxonomic variety of the microflora. The importance to the microflora of differences in resource quality is apparent from the measurement of the community activity as weight loss or respiration, but the composition and characteristics of the community are implicit, not explicit. The hidden changes in species diversity and structure of the microbial community during resource decomposition were analyzed by Swift (78). He provided a general hypothesis that the declining availability and variety of substrates during decomposition is partly compensated by increased physical diversity of the resource, allowing development of a secondary microflora of bacteria and actinomycetes to replace the fungi which dominate the litter habitats. This recognizes the response of the microflora to the modification of the resource during decomposition and to the presence of other organisms.

The central idea of a succession of microflora is an old one, linked to Winogradsky's (90) concept of different growth strategies of zymogenous and autochthonous microflora. However, the continued development of the ideas of the

selection of growth strategies in plants and animals in response to varying environments can help to clarify the pattern of carbon and energy utilization by microflora and fauna on the basis of their response to the three identified groups of factors: (i) resource quality, (ii) physicochemical environment, and (iii) other organisms. The response is in the selection of combinations of characteristics of growth, reproduction, and physiology.

Some parallel between microbial strategies and those of plants and animals might be expected because (i) they are responding to common climatic conditions, at least at the macroscale, and (ii) the selection of plant strategies determines the quality of resource input, for example, through the proportion of photosynthate allocated to plant parts, the longevity of these parts, and associated characteristics of nutrient resorption and herbivore and pathogen defense.

Within plant and animal ecology, two main axes or gradients in the environment are recognized: durational stability and adversity (74). *Durational stability*, or frequency of disturbance, selects for species characteristics along the *r-K* continuum (51), linked to succession at the community level and to characteristics of energy and nutrient flow at the ecosystem level (63). *Adversity*, the degree of favorableness and constancy of a resource, is increasingly recognized as modifying the species characteristics which are selected from within the *r-K* gradient. Climatic severity and nutrient availability are seen as varying along the adversity axis (29, 34, 35, 52, 74, 88). Thus, three types of strategies have been identified in response to the two axes: (i) *exploitation*, basically the *r* strategy, occurring in favorable situations subject to disturbance; (ii) *interaction*, basically the *K* strategy, in which favorable conditions prevail for long periods relative to the organism's life cycle; and (iii) *adversity* (*A*), in which conditions are predictably severe with short and infrequent periods suitable for growth and reproduction. In his extensive analysis of plant strategies, Grime (35) identified stress tolerance as a strategy distinct from the *r-K* continuum evolved in intrinsically unproductive habitats, including climatic severity, or under conditions of extreme resource depletion induced by the vegetation itself. However, he suggested that "ruderal" and "stress-tolerant" strategies correspond, respectively, to the extremes of *r* and *K* selection and that a "competitive" strategy is recognizable in an intermediate position.

The concepts of habitats of varying durational stability and adversity, and the associated selection of exploitation, interaction, and adversity strategies can be translated into microbial ecology (9, 28, 42, 66, 78). The scale difference in time and space is obviously important. The key resource to which the microflora respond is organic matter which, through litter input and root growth, provides recurrent habitats for colonization and growth. In this sense the recurrent provision of resources can be equated with disturbance, allowing the opportunity for successional development, rather than through loss or dilution of microbial biomass as argued by Pugh (66).

On resources of high quality in temperate and nonarid tropical environments, i.e., favorable habitats, selection for exploitation strategies (*r*) in the early stages of decomposition should be strongest, followed by a longer period in which interaction strategies (*K*) are expected to dominate. Resources of low quality, resulting from recalcitrant carbon substrates, low nutrient concentrations, or high concentrations of inhibitory compounds, can be equated with conditions of continuous adversity or stress, in contrast to discontinuous climatic adversity characteristic of arid and cold environments. Limited discontinuous climatic adversity may also occur in otherwise favorable habitats, but on a time scale relevant to the microflora, for example, drying of surface litters in temperate regions.

The microbial characteristics which are selected for under various conditions are summarized in Table 4. It must be emphasized that (i) most habitats do not fall at the extremes of resource quality and will therefore select for less marked characteristics, (ii) selection will be for combinations of characters, all of which will not necessarily be present at the same time, (iii) fluctuations in climatic conditions or grazing over short time periods can allow species with different growth characteristics to coexist, and (iv) there is a strong stochastic element, particularly during colonization, which may reverberate through the subsequent sequence of organisms. A detailed examination of existing relevant information is not feasible here, but the principles will be illustrated by reference to particular resource types.

High resource quality, favorable environment. Roots, like herbaceous leaves, provide recurrent input of substrates, with a considerable proportion of low-molecular-weight compounds, on which the growth characteristics of the succession of organisms show a sequence from exploitive (*r*) to interactive (*K*) strategies as identified by Bowen (9). Pseudomonads, capable of utilizing a wide range of substrates, are common colonizers migrating along the developing root or, particularly in the case of roots of annual plants, colonizing from the soil. A generation time of 5.2 h was recorded for *Pseudomonas* sp. on *Pinus radiata* roots (9). Such short generation times link with high yield coefficients (85), al-

TABLE 4. Trends in microbial characteristics in early (exploitation) and late (interaction) stages of succession under favorable conditions and under conditions of continuous resource or discontinuous climatic adversity

Characteristic	Exploitation (*r*)	Interaction (*K*)	Adversity (*A*)	
			Continuous (resource)	Discontinuous (climate)
Morphology	Small cells or diffuse mycelium.	Large; often compact mycelium. Cell walls resistant to animal enzymes.	Large cells; compact mycelium.	Large or small.
Physiology	Rapid growth rate, high yield efficiency, giving maximum colonization. Use readily available substrates. Nutrient demanding. Sensitive to plant defense compounds.	Moderate growth rate and yield efficiency for substrate utilization. Use of more resistant substrates. Moderately nutrient demanding. Production of defense compounds (antibiotics) against competitors and grazers.	Slow growth rate, low yield efficiency for maximum use of recalcitrant substrates and nutrient conservation. Intraspecific responses common. Sensitive to chemical stimuli; resistant to plant defense compounds.	Tolerant of low temperature or moisture or rapid metabolic increase with temperature. Sensitive to climatic stimuli.
Life history	Simple. Maximum production of wind- and water-dispersed propagules following short growth phase. Sporing intermittent.	Varied.	Production of larger, resistant propagules with energy and nutrient reserves. Long growth phase. Seasonal dispersal.	Either long tolerant growth phase or short growth from resistant dormant stage. Dormancy linked to climate.
Population dynamics	Explosive, density independent, crash through substrate depletion or opportunistic grazing.	Relatively damped, density-dependent control by interspecific competition and selective grazing.	Relatively damped, control by intraspecific competition and selective grazing.	Erratic, climatically controlled.
Community structure	Diverse.	Symbiotic relations extensive. Very diverse.	Symbiotic associations intimate. Low diversity.	Low diversity.

lowing rapid biomass expansion, although less than 10% of the surface is usually occupied (9). Pseudomonads are particularly consumed by soil amoebae (37), and grazing can cause drastic reduction in laboratory and field populations, with increased nutrient release (14, 15).

Behind the apex, with lower exudation, fungal growth may predominate, growth rates of 3 mm/day being much slower than root extension (9 mm/day) in *Vicia faba* (81). The slower growth rate of *Bacillus* sp. (39 h) on *P. radiata* (9), lower consumption by amoebae (37), and the production of endospores are indicative of an interactive (*K*) strategy compared with the pseudomonads. The species associations and interactions are complex (9), but at least in some cases, a clearer pattern emerges after death. Excision of *V. faba* roots was followed by a fungal sequence from "sugar fungi" (e.g., *Pythium, Mucor, Penicillium*) to cellulolytic types (e.g., *Chaetomium, Humicola*) on well-decomposed roots after a few weeks (53), and Stenina (75) observed actinomycetes commonly in late stages of decay.

The simplistic generalizations given here are not satisfactory, and a more comprehensive analysis of fungal strategies is given by Pugh (66). A main limitation on such an analysis is the lack of information which combines the range of organisms and attributes concerned. Basic information on growth characteristics for bacteria in laboratory culture is extensive, as is taxonomic information on fungi in the field; a more balanced picture is needed. However, the sequence of yeasts, sugar fungi, ascomycetes, fungi imperfecti, and basidiomycetes on high-quality resources (27) remains a partially validated model of the *r-K* sequence. Deviations from this model may be related to variations in adversity, considered next.

Increasing adversity of resource quality. Increasing adversity in resource quality, with in-

creasing proportions of ligno-cellulose, decreasing nutrient content, and varying secondary compounds, is represented along a gradient from herbaceous leaf litter, conifer needles, bracken petioles, and deciduous and coniferous wood, to the extreme substrate, homogeneous, recalcitrant keratin.

Consideration of fungal development on the needles of pine identifies the influence of adversity in terms of nutritional quality and inhibitory secondary compounds (47). Common primary saprophytes play only a very small part in the decomposition of *Pinus sylvestris* litter because of its chemical nature. The needles contain little available sugar and high lignin, and many of the cytoplasmic proteins and starch are "locked up" by tannins (56, 57). The free phenolics inhibit fungal growth, and the cuticle provides an effective physical barrier. Stomata and the needle bases provide important entry points for the specialists *Lophodermium pinastri* and *Fusicoccum bacillare* (46), and a subcuticle breakdown of cellulose is commenced. *Marasmius androsaceus* has the ability to surface colonize the needles from rhizomorphs and then sends out small hyphae which degrade, and pass through, lignified walls into the xylem. This organism may overcome nitrogen limitation by translocation and is clearly resistant to the monoterpenes. After the tissue has been colonized by microorganisms, the cryptostigmatid mites become the dominant fauna, feeding mainly on hyphae and thus avoiding the problems of nutrient paucity and inhibitory terpenes.

A similar "abbreviated" succession was described during the decomposition of bracken petioles (25), so-called because the classic *r-K* pattern (27) for plant material was modified on this more adverse substrate, with the *r* phase missing and with colonization and subsequent decomposition being of a *K* form. Adversity is primarily a result of the resorption and leaching of nutrients and soluble sugars from the petiole prior to decomposition, leaving a resource which requires the import of nitrogen, and possession of enzymatic machinery for degradation of structural carbohydrates, even at the initial decay stage. The sphaeropsidales and basidiomycetes such as *Mycena galopus* are favored, and the decay process is slow. Since yield efficiency at slow growth rates is poor (85), the amounts of biomass supported by adverse substrates are proportionately low, and yield coefficients as low as 0.04 for *Mycena* growing on oak litter have been presented. In *r* strategy fungi and bacteria with coefficients of anything up to 0.60 to 0.70 (26, 77) are possible, but the strategies of nutrient translocation, degradation of inhibitory substances, maintenance of large biomass, and utilization of recalcitrant molecules all lead to yield inefficiency.

Of the abundant natural substrates, wood is perhaps the most adverse, being low in nutrients, structurally homogeneous, rich in inhibitory secondary compounds, and low in available carbohydrate, and having small surface area. The tight links between fungal tolerance to phenolics and nature of substrate decomposed reflect the importance of monoterpenes in deciding succession on different types of wood (43), with the ability to grow at high CO_2 concentrations distinguishing between wood and litter basidiomycetes.

The strong interactions shown by basidiomycetes on wood include interactions not only with substrates but also between species and between individuals within species. The interactions with substrate are perhaps best illustrated by Kirk and Fenn (48), who showed that ammonium nitrogen and certain amino acids may repress lignolytic activity in basidiomycetes, providing a chemical signal preventing premature, and unprofitable, entry into the succession. Rayner and co-workers have shown clearly the intraspecific and intense antagonism between individuals colonizing wood, interactions developing which are not present in more generalized *r* types of organisms (e.g., A. D. M. Rayner and J. E. Webber, *in* D. H. Jennings and A. D. M. Rayner, ed., *The Fungal Mycelium*, in press). Their work, and that of Thompson and Boddy (82), has altered the concept of the individual when considering basidiomycete growth, and we now realize that a single individual may ramify through the litter over areas of square meters, with inherent consequences for nutrient translocation and substrate exploitation.

The grazing of fungal mycelium by fauna is a key feature in successional development. In wood, animal grazing may disturb a *K* strategist and provide fresh substrate for rapid bacterial and "*r*"-type mycelial development (79). This is paralleled by the effects of animal grazing in litter (2). K. Newell (Soil Biol. Biochem., in press) showed, in an analysis of growth and distribution of *Mycena galopus* and *Marasmius androsaceus*, that grazing by the collembolan *Onychiurus latus* dictated the outcome of the competition. *Marasmius* readily outgrows *Mycena* in litter and fermentation layer material from oak woodlands, as well as in culture. When the two organisms are grown together in litter and fermentation layer material in the absence of the grazer, this trend continues, and *Marasmius* outcompetes *Mycena*. In the presence of the grazer, which prefers *Marasmius* as a food source, the competition is reversed, and *Mycena* dominates. In the field *Marasmius* is restricted to the litter layer, where *O. latus* is least common, and the distribution of *Marasmius* and

Mycena can be explained in relation to growth rate and grazing.

Adversity through climatic severity. The discontinuous stress of cold and arid environments imposes two main problems on the microflora: survival during adverse conditions has to be combined with maximizing growth during the short favorable period. Superimposed on this is a tendency for plants under adverse conditions to produce secondary compounds to protect long-lived photosynthetic structures; a high content of aromatic compounds is recognized in many desert plants. Although no comprehensive data are available, there are some important indications, particularly from tundra studies (23, 70), of strategies adopted by the microflora under temperature stress.

Enzymatic capacities of bacteria and fungi on standing dead litter and in soil in tundra are unexceptional, but selection from a wide range of strategies in response to the different microhabitat temperature regimes is indicated. Linear responses can sustain activity over a wide temperature range, and an exponential response can enhance activity during short periods of favorable temperature. Among the fungi a variety of temperature-response curves were shown for respiration, growth, and substrate utilization (23). Respiration, and possibly cellulose and phenol oxidation, is continued to −7.5°C, with growth down to 0°C. Temperature-substrate responses may be linked to the spring thaw when some yeasts, bacteria, and algae capitalize on the dissolved organic carbon and nutrients released through freeze-thaw cycles (60, 91). Overwintering strategies of the microflora are not as clear as for invertebrates, for which, interestingly, Block (8) found that the biology of the mite *Alaskozetes* did not readily fit into the *r-K* continuum in its responses to climatic adversity.

Intimate symbiotic relationships may represent one *A* strategy in dry conditions, microflora obtaining an advantage of an improved microclimate when associated with termitaria (50) or invertebrate guts (12). A similar strategy is advantageous under resource adversity, either carbon or nutrient, and is seen in gut microflora (12, 61), mycorrhizal associations, and lichens.

CONCLUSIONS

The general comparison of carbon and energy fixation and dissipation between biomes emphasizes two features: (i) broad climatic control, with heterotrophic activity closely following plant production, and (ii) the similarities, in all but quantity, with belowground production often compensating the more obvious aboveground growth. The differences between ecosystems appear at a finer scale, in functional, rather than species, characteristics. Here again, there is evidence that the heterotrophs mirror the plants in terms of growth strategies through (i) their direct response to variation in quality of resource input which is determined by plant growth strategies and (ii) their similarity of response to common environmental conditions.

The hypotheses of growth strategies in microbial communities are, as yet, poorly developed. This is largely because of the versatility and variety of the microflora which provides a multitude of combinations of options to cope with the variations in resource input and environment. However, there is a reasonable theoretical basis for the selection of recognizable combinations of morphological, physiological, and phenological features within the microbial associations in different habitats. The pattern will rarely be precise because of chance, environmental fluctuation, and microbial variety, but the earlier hypotheses of the *r-K* continuum are made more relevant to microbial ecology when a dimension of adversity or stress is added to that of disturbance.

There are also indications that the microbial growth strategies selected in different habitats will have a feedback effect on plant growth. The efficiency of bacterial biomass production per unit of organic substrate consumed depends on the type of energy metabolism involved, growth rate, kind of substrate limitation, and degree of predation. There is a shift from biomass formation to nutrient cycling with decreasing growth rate (85). Extended to other microflora, the slow growth rates associated with low resource quality may compensate for mechanisms of nutrient conservation and result in increased nutrient release per unit of substrate decomposed, compared with high-quality resources. Such interrelationships of processes resulting from selection for microbial growth strategies need to be explored quantitatively. However, is it unreasonable to speculate that the selection of different growth strategies in the microflora may account, for example, for the direct relationship shown by Berg and Staaf (5) between the initial nitrogen concentration (resource quality) and the concentration at which net nitrogen mineralization occurs, and for the much lower C/N ratio required for nitrogen availability to plants in arable conditions compared with low-quality forest floor litters (41)?

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